

# Microzooplankton grazing and nitrogen supply of phytoplankton growth in the temperate and subtropical northeast Atlantic

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**ABSTRACT:** Serial dilution experiments were conducted on JGOFS-North Atlantic cruise of RV 'Meteor' M36/2 at a 20° W transect in June and July 1996 to assess the role of microzooplankton grazing and nitrogen supply in controlling phytoplankton stocks in the subtropical and temperate northeast Atlantic. Rates of microzooplankton grazing ranged from 0.08 d<sup>-1</sup> at 54° N to 0.53 d<sup>-1</sup> at 40° N and mean growth rates of phytoplankton ranged from 0.19 d<sup>-1</sup> at 54° N to 0.75 d<sup>-1</sup> at 40° N. Both rates were positively related to seawater temperature, whereas the apparent growth yield of phytoplankton declined with increasing temperature from 0.19 µg chl a dm<sup>-3</sup> d<sup>-1</sup> at 54° N to 0.01 µg chl a dm<sup>-3</sup> d<sup>-1</sup> at 33° N. Complete nitrogen saturation of phytoplankton growth indicated light or non-nitrogenous limitation at the nitracline at 47° N and in the deep chlorophyll maximum at 33° N, whereas in the mixed layer at 47° N and 54° N the ambient nitrogen supply was sub-saturated and yielded 63 and 39% of nitrogen-saturated growth. Nitrogen supply of phytoplankton growth was dominated by external and cellular sources in nitrate-rich waters of the mixed layer at 54° N and at the nitracline at 47° N, whereas nitrogen regeneration dominated at the nitrate-depleted surface waters at 47° N. However, in the deep chlorophyll maxima at 33° N and 40° N phytoplankton growth was primarily maintained by nitrogen regeneration, although external nitrogen was sufficiently available. The recycling efficiency of the microbial community was defined as the ratio of regenerated growth yield to herbivorous grazing loss. Efficiencies of ~100% under post-bloom situations indicated tight coupling of predation, nitrogen supply and phytoplankton growth. We suggest that microzooplankton grazing has a high potential for nitrogen supply and biomass control of phytoplankton communities during summer in the temperate and subtropical northeast Atlantic.

**KEY WORDS:** Microbial food web · Nitrogen supply · Recycling efficiency · Northeast Atlantic

## INTRODUCTION

Microzooplankton grazing has received much attention in marine and freshwater ecology and is now considered a key process of aquatic food webs due to its impact on phytoplankton and bacterial communities, and the potential for nutrient regeneration (Goldman et al. 1985, Caron & Goldman 1990, Suzuki et al. 1996). The serial dilution assay by Landry & Hassett (1982) has been frequently applied to estimate community grazing rates and potential growth rates of phytoplankton (Burkill et al. 1993a, Verity et al. 1993, Strom

& Strom 1996). A critical assumption for the application of the method is that dilution has no differential influence on the nutrient supply of phytoplankton growth, a problem that is generally met by adding potentially limiting nutrients to all incubation bottles. However, Andersen et al. (1991) perceived that all principal nutrient sources (external, cellular and regenerated nutrients) cause different dilution responses of the phytoplankton growth rate. They realized the inherent potential to analyze nutrient supply of phytoplankton growth and developed a theoretical framework to estimate the contributions of nutrient regeneration, cellular reserves and external nutrients for the nutrient supply of phytoplankton growth in nutrient-impo-

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We have applied their model with modifications to situations where nutrient uptake during incubation only causes small changes of the external nutrient pool that have no significant effect on the growth rate of the phytoplankton community. Furthermore we considered a threshold level of regeneration in cases where regeneration ceased below a certain plankton density. A cruise to the North Atlantic during summer 1996 provided us the opportunity to apply the dilution assay to an experimental study of the trophic interaction between microzooplankton grazing, nutrient supply and phytoplankton growth. The experiments were carried out over a meridional transect at 20° W, where plankton communities and nutrient regimes were at different seasonal stages of development.

## MATERIAL AND METHODS

**Experimental set-up.** Serial dilution experiments were carried out at 4 stations on a 20° W longitudinal transect during the German JGOFS North Atlantic cruise M36/2 of RV 'Meteor'. Details of the positions and sampling conditions are given in Table 1. The experimental procedures for the determination of microzooplankton grazing essentially followed the protocol of Landry & Hassett (1982) and Landry (1993). Estimations of the nutrient supply for phytoplankton growth were calculated by a modified version of the non-linear model of Andersen et al. (1991).

Four dilutions in the range of 25 to 100% unfiltered seawater were prepared from seawater that was gently screened through a 300 µm mesh and seawater from the same source that was passed through glass-fibre filters (Whatman GF/F). Two series of nutrient-enriched dilution experiments were conducted: Series I incubations received a full nutrient supplemented with 10 µM NH<sub>4</sub>Cl, 1 µM KH<sub>2</sub>PO<sub>4</sub>, 5 µM Si(OH)<sub>4</sub>, 1 µM Na<sub>2</sub>EDTA, 0.1 µM FeSO<sub>4</sub> and 0.01 µM MnCl<sub>2</sub>; Series II incubations were not nitrogen-enriched but otherwise received the same amount of nutrients and chelators as Series I. Duplicate samples for nutrient analysis were taken prior to nutrient enrichment.

Two or 4 subsamples of each dilution were incubated in 2.5 l polycarbonate bottles, on-deck, in a dark-lined basin with a constant flow of seawater from the mixed layer. *In situ* light intensities were simulated by layers of neutral density filters (GamColor®) with transmissions of 2.3 to 50% averaged over the photosynthetically active range (PAR) of irradiance, the transmissions averaged over the UV-B range (290 to 320 nm) of irradiance accounted for <20% of the transmissions in PAR. The surface PAR irradiance was constantly measured by a 2π-quantum sensor (LI-COR®) and was recorded by an internal datalogger. The average *in vitro* irradiance ( $I_{iv}$ ) was determined as the product of the filter transmission and the average surface PAR irradiance during incubation.

All experiments were started just before dawn and were terminated after 24 h. Three initial ( $t_0$ ) samples for chlorophyll *a* (chl *a*) were taken from each dilution to determine the relative plankton density ( $x$ ). Two samples were taken from each bottle on termination of the experiments. Samples for chl *a* were filtered onto Whatman GF/F filters under low vacuum and were frozen immediately.

**Analytical.** Nutrient concentrations were determined by means of an autoanalyser after the methods of Hansen & Koroleff (1999). The chl *a* content was determined fluorometrically as described by Herbrand et al. (1985). Filters were extracted in 90% acetone, homogenised, centrifuged and measured in a Turner Designs Fluorometer. The depth of the euphotic zone was defined as the horizons of 1% incident surface irradiance and was calculated by a bio-optical model adapted from Morel (1988) and using actual profiles of chl *a* from our study.

**Rate estimates. Apparent growth rates:**  $r(x, t)$  were described by an exponential growth equation, as a function of the relative plankton density ( $x$ ), defined as the fraction of unfiltered seawater, and the duration of the incubation ( $t$ ):

$$r(x, t) = \frac{1}{t} \cdot \ln \left[ \frac{C(x, t)}{C(x, 0)} \right] \quad (1)$$

Table 1. Position of the stations, depth of the fluorescence maxima where seawater for dilution experiments was sampled and chlorophyll *a* and nutrient concentrations at the fluorescence maxima

Position	Date (1996)	Depth (m)	Chl <i>a</i> (µg dm <sup>-3</sup> )	NO <sub>3</sub> <sup>-</sup> (µmol dm <sup>-3</sup> )	N <sub>2</sub> O <sub>3</sub> <sup>-</sup> (µmol dm <sup>-3</sup> )	PO <sub>4</sub> <sup>3-</sup> (µmol dm <sup>-3</sup> )	Si(OH) <sub>4</sub> (µmol dm <sup>-3</sup> )
33° N, 21° W	27 Jun	110	0.21	1.74	0.01	0.11	0.42
40° N, 20° W	2 Jul	60	0.39	0.43	0.04	0.07	1.02
47° N, 20° W	5 Jul	30	0.95	1.31	0.08	0.19	0.05
47° N, 20° W	7 Jul	8	0.99	0.05	0.03	0.08	0.00
54° N, 20° W	12 Jul	8	1.58	2.79	0.09	0.26	0.00

where  $C(x,0)$  and  $C(x,t)$  are initial and final concentrations of chl *a* at a series of dilution experiments. The relative plankton density ( $x$ ) was determined by  $C(x,0)/C(1,0)$ , e.g. the ratio of initial chl *a* concentrations in diluted and undiluted seawater.

**Grazing coefficients:** ( $g$ ) were estimated as the slope of linear regressions to apparent growth rates ( $r$ ) versus relative plankton density ( $x$ ) according to the model of Landry & Hassett (1982) from below:

$$r(x) = \mu_{\max} - g \cdot x \quad (2)$$

where the potential growth rate  $\mu_{\max}$  is assumed to be independent of dilution in experiments with complete nutrient enrichment (Series I).

**Mean growth rates at ambient nitrogen concentration:** For experiments without nitrogen enrichments (Series II), we assumed that phytoplankton growth is affected by dilution if growth is supplied by regenerated nitrogen from microzooplankton grazing and if external nitrogen is not sufficiently available. The mean growth rate ( $\bar{\mu}_N$ ) in such experiments is a time-weighted average over the duration of the incubation and was estimated after Andersen et al. (1991) by:

$$\bar{\mu}_N(x) = r_N(x) + g \cdot x \quad (3)$$

where  $r_N$  is the apparent growth rate from experiments with nitrogen-free nutrient enrichments and the grazing coefficient  $g$  derives from the dilution experiment with complete nutrient enrichment (Series I).

#### Regenerated, external and cellular nitrogen supply:

The mean growth rate at the relative plankton density  $x$  over the duration  $t$  can be expressed in terms of the total growth yield  $\Delta C(x,t)$  after Andersen et al. (1991) by:

$$\bar{\mu}_N(x) = \frac{1}{t} \cdot \ln \left[ \frac{C(x,0) + \Delta C(x,t)}{C(x,0)} \right] \quad (4)$$

The total growth yield is based on the availability of nitrogen from 3 principal sources: (1) the cellular nitrogen reserves of phytoplankton present at the start of the experiment, (2) the initial concentration of dissolved nitrogen, and (3) nitrogen that is recycled during the incubation by microzooplankton grazing. Therefore the growth yield of undiluted plankton  $\Delta C(1,t)$  includes the growth yield from internal nitrogen reserves  $\Delta C_i(1,t)$ , the growth yield from external nitrogen pool  $\Delta C_E(1,t)$  and the regenerated growth yield  $\Delta C_R(1,t)$ . The external nutrient pool will be unaffected by dilution (Fig. 1, top panel: B and B\*) whereas the cellular nitrogen reserves and the abundance of grazers and their food are reduced proportionally by dilution at the factor  $x$  (Fig. 1, top panel: A and A\*). At a constant clearance rate the amount of nitrogen regenerated depends on the density of grazers and their prey and will therefore be proportional to  $x^2$

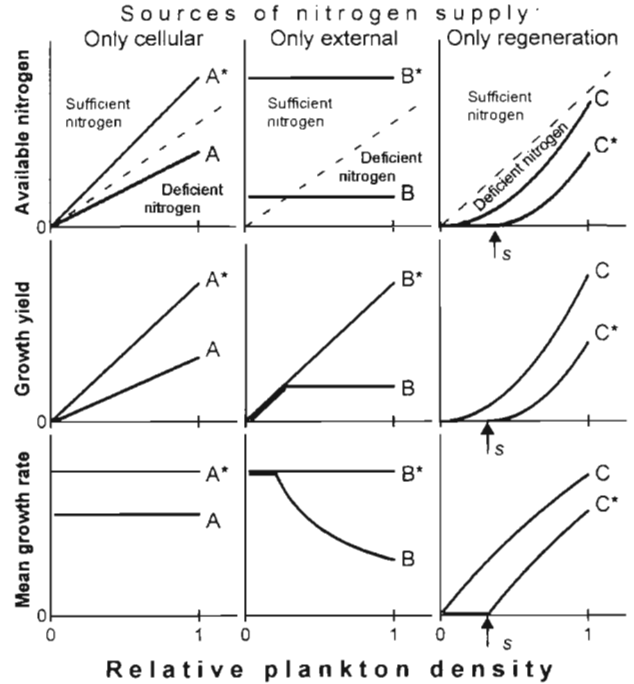


Fig. 1. Model calculation for the dilution response of total cellular nitrogen, external nitrogen and nitrogen regeneration as well as corresponding growth yields  $[\Delta C(x)]$  and mean growth rates  $[\bar{\mu}_N(x)]$  from these sources according to Eq. (6) and Eq. (8). Dashed line indicates the nitrogen demand of phytoplankton at ambient growth conditions. Arrow in case C indicates the threshold density of nitrogen regeneration ( $s$ ). Note that the dilution response of the available nitrogen is different in cases A, A\* and B\*, whereas the corresponding mean growth rates are unaffected by dilution

(Fig. 1, top panel: C). Nutrient regeneration hence decreases exponentially with dilution and will cease at a threshold density  $s$ , where the food uptake either ceases (Strom 1991) or just meets the minimum metabolic requirements of the grazers without any surplus to be excreted (Rothhaupt 1995). (Fig. 1, top panel: C\*). Above this density ( $x \geq s$ ) the amount of nutrients regenerated by grazers will be proportional to  $(x - s)^2$ .

Andersen et al. (1991) expressed the total growth yield as a function of the relative plankton density ( $x$ ) by the following polynomial equation:

$$\Delta C(x,t) = \Delta C_R(t) \cdot x^2 + \Delta C_I(t) \cdot x + \Delta C_E(t) \quad (5)$$

They restricted the validity of the quadratic argument to very short incubations since the regeneration of nutrients by grazers depends on the nutrient content of their food that might change during the incubation. Eq. (5) describes the total growth yield  $\Delta C(x,t)$  under conditions where the growth yield from the external nitrogen  $\Delta C_E(x,t)$  is limited by the amount of dissolved nitrogen (Fig. 1, middle panel: B). However, if the external nitrogen concentration is large compared to

the uptake during incubation, the changes of external nitrogen concentration will hardly affect  $\Delta C_E(x, t)$ . In this case of sufficient external nitrogen its growth yield will depend on the initial phytoplankton biomass and hence will increase proportionally with the relative plankton density  $x$  (Fig. 1, middle panel: B\*). We modify Eq. (5) accordingly and write Eq. (6):

$$\Delta C(x, t) = \Delta C_R(t) \cdot (x - s)^2 + \Delta C_I(t) \cdot x + \Delta C_{Es}(t) \cdot x + \Delta C_{Ed}(t) \quad (6)$$

for  $x \geq s$

The refined expression differentiates between growth yields from deficient external nitrogen,  $\Delta C_{Ed}(x, t)$  where the external nitrogen pool is depleted during incubation and growth yields from sufficient external nitrogen,  $\Delta C_{Es}(x, t)$ .

If the right side of Eq. (6) is introduced into Eq. (4), and if the initial phytoplankton biomass of an individual dilution  $[C(x, 0)]$  is substituted by the equivalent product  $[xC(1, 0)]$  of the initial phytoplankton biomass  $[C(1, 0)]$  and the relative plankton density ( $x$ ), we obtain Eq. (7):

$$\bar{\mu}_{-N}(x) = \frac{1}{t} \cdot \ln \left[ 1 + \frac{\Delta C_R(t) \cdot (x - s)^2 + \Delta C_I(t) \cdot x + \Delta C_{Es}(t) \cdot x + \Delta C_{Ed}(t)}{x \cdot C(1, 0)} \right] \quad (7)$$

for  $x \geq s$

According to Andersen et al. (1991) we simplified Eq. (7) by normalising the growth yield  $\Delta C_Z(x, t)$  from each nutrient source  $Z$  with the initial phytoplankton biomass  $C(x, 0)$ , and denoted the specific growth yield  $K_Z(x) = \Delta C_Z(x, t) / x \cdot C(1, 0)$  from  $Z$ , which in Eq. (8) expresses specific growth yields from regenerated nitrogen  $[K_R(x)]$ , cellular nitrogen reserves  $[K_I(x)]$ , sufficient external nitrogen  $[K_{Es}(x)]$  and deficient external nitrogen  $[K_{Ed}(x)]$ .

$$\bar{\mu}_{-N}(x) = \frac{1}{t} \cdot \ln(1 + K_R \cdot (x - s)^2 \cdot x^{-1} + K_I + K_{Es} + K_{Ed} \cdot x^{-1}) \quad (8.1)$$

for  $x \geq s$

$$\bar{\mu}_{-N}(x) = \frac{1}{t} \cdot \ln(1 + K_I + K_{Es} + K_{Ed} \cdot x^{-1}) \quad (8.2)$$

for  $x \leq s$

The characteristics of this expression are depicted in Fig. 1 (bottom panel) where the mean growth rate was calculated individually for each nitrogen source as a function of  $x$ . The actual dilution response of  $\bar{\mu}_{-N}$  depends on a combination of different nitrogen sources and provides the basis of our estimates. However, since the specific growth yields from cellular reserves  $[K_I(x)]$  and from sufficient external nutrients  $[K_{Es}(x)]$  are both independent of the relative plankton density and hence are constants in Eq. (8), they cannot be estimated separately. Therefore  $K_I(x)$  and  $K_{Es}(x)$  were merged into a single coefficient  $K_{Di}(x)$ , denominated as the density-independent specific growth

yield.  $K_{Di}(x)$  can be interpreted as a specific growth yield due to cellular nutrient reserves  $[K_I(x)]$  only if all externally dissolved nitrogen is virtually exhausted, which might be difficult to demonstrate since half-saturation constants for dissolved inorganic nitrogen of most oceanic algae approach the detection limit of standard analytical techniques (Harrison et al. 1996).

After multiplication with  $t$ , exponentialisation and multiplication with  $x$  on both sides of Eq. (8), we obtain the final analytical equations that describe the total specific growth yield as a function of  $x$  and  $t$ :

$$x \cdot (e^{t \cdot \bar{\mu}_{-N}(x)} - 1) = K_R \cdot (x - s)^2 + K_{Di} \cdot x + K_{Ed} \quad \text{for } x \geq s \quad (9.1)$$

$$x \cdot (e^{t \cdot \bar{\mu}_{-N}(x)} - 1) = K_{Di} \cdot x + K_{Ed} \quad \text{for } x \leq s \quad (9.2)$$

Without a detectable threshold we determined the coefficients of Eq. (9.1) with  $s = 0$  by curvilinear regression analysis according to Sokal & Rohlf (1995). If only  $K_{Di}$  and  $K_{Ed}$  or  $K_R$  and  $K_{Di}$  were significant, they were determined after exclusion of insignificant parameters by linear regression analysis. Otherwise if a threshold was detectable,  $K_{Di}$  and  $K_{Ed}$  were calculated by linear regression analysis of Eq. (9.2) and were subsequently introduced into Eq. (9.1), where  $K_R \cdot (x - s)^2$  was isolated and then linearised by root extraction that allowed the determination of  $s$  and  $K_R$  by linear regression analysis.

To detect and estimate the threshold density of nutrient regeneration ( $s$ ), 3 different dilution responses, depending on interactions with other nutrient sources, should be considered:

Case 1: If growth is also supplied by cellular reserves or sufficient external nitrogen,  $\bar{\mu}_{-N}(x)$  would be constant below  $s$  (Eq. 9.2) but would increase above  $s$ , at the onset of regeneration (Eq. 9.1). In this case, a virtual point just below the dilution, where the mean growth rate increases with increasing  $x$ , was taken to separate the validity ranges of Eqs. (9.1) and (9.2). The growth yields  $K_{Di}$  and  $K_{Ed}$  were then calculated by linear regression of Eq. (9.2) and were subsequently introduced into Eq. (9.1) to determine  $s$  and  $K_R$  by curvilinear regression. Alternatively, the regenerated growth yield  $[K_R(1)]$  can be determined from the difference:  $K_R(1) = [x \cdot (e^{t \cdot \bar{\mu}_{-N}(1)} - 1)] - K_{Di}(1) - K_{Ed}(1)$ .

Case 2: If growth is supplied by regeneration and a deficient external nitrogen source, the inverse dilution responses of  $K_R(x)$  and  $K_{Di}(x)$  cause an intermediate minimum of  $\bar{\mu}_{-N}(x)$  as shown by Andersen et al. (1991; Fig. 1). In this case a plot of Eq. (9.1) could reveal a threshold, since it is a linear function for  $x \leq s$ , whereas an intermediate onset of a quadratic increase would indicate the delayed onset of regeneration and the approximate location of the threshold. However, this probably requires higher  $x$  resolution than applied at this preliminary study to reveal a threshold in this context.

Case 3: If regeneration is the only significant nitrogen source, a threshold is directly indicated by the zero growth intercept at the x-axis (Fig. 1: C and C\*). This case was found in experiments by Gaul & Koeve (unpubl. data).

*Microzooplankton grazing* comprises losses from the initial phytoplankton biomass and from the growth yield. Therefore we described the specific biomass loss of phytoplankton due to microzooplankton grazing by a specific coefficient  $K_G$  that derives from the turnover rate of the phytoplankton stock by microzooplankton grazing  $(1 - e^{-g})$  weighted by the mean growth rate  $(e^{\bar{\mu}_N})$ :

$$K_G = e^{\bar{\mu}_N} (1 - e^{-g}) \quad (10)$$

*Growth yields and total biomass loss* of phytoplankton were calculated as the product of the initial phytoplankton biomass  $[C(1, 0)]$  and a coefficient  $K_i$  that represents either a specific growth yield  $[K_R(1), K_{Di}(1), K_{Ed}(1)]$  or the specific daily grazing loss ( $K_G$ ):

$$B_i = K_i \cdot C(1, 0) \quad (11)$$

where e.g.  $B_R$  is the daily growth yield from nitrogen regeneration and  $B_G$  is the daily biomass loss of phytoplankton due to microzooplankton grazing.

The recycling efficiency of the microbial community was estimated by the ratio of the regenerated growth yield and the total microzooplankton grazing loss of phytoplankton  $B_R/B_G$ .

**Nitrogen saturation of phytoplankton growth.** The ratio of the mean growth rate  $\bar{\mu}_N(1)$  from Series II experiments without nitrogen enrichment and the potential growth rate  $\mu_{max}$  from Series I experiments with full nutrient enrichments was taken as an indicator of nitrogen saturation  $Q_N$  of phytoplankton growth. For  $Q_N \approx 1$  we assumed that the nitrogen supply was saturated and that phytoplankton growth was controlled by light or other nutrients. Since  $PO_4^{3-}$  enrichments of primarily P-limited communities, or  $Si(OH)_4$  enrichments of partly Si-limited communities might induce nitrogen limitation where nitrogen is just a secondary limiting factor (Hecky & Kilham 1988), the  $Q_N$  value primarily indicates the degree of nitrogen saturation.

## RESULTS

### Accuracy of growth rate estimates and regression models

The difference between growth rate averages and the outcome of the model regression  $[\Delta r(x)]$  was attributed to measurement errors, the variance of replicated experiments and the deviation of the model regression

from the real dilution response of  $r(x)$  or  $\bar{\mu}_N(x)$ . If we consider the analytical variance due to measurement errors ( $S_{ana}^2$ ), the experimental variance of replicated incubations ( $S_{exp}^2$ ) and the deviations of the regression model ( $S_{mod}^2$ ) to be normally distributed, which is probably just an approximation for the latter, we can write the following expression

$$S_{reg}^2[\Delta r(x)] = S_{ana}^2[r(x)] + S_{exp}^2[r(x)] + S_{mod}^2[r(x)] \quad (12)$$

where the regression variance,  $S_{reg}^2[\Delta r(x)]$ , should describe the total deviation of the apparent growth rate estimate from the linear regression in Series I experiments. The regression variance of non-linear regressions in Series II experiments was described analogously.

The analytical variance of the apparent growth rate estimate in a single experiment is due to the measurement error of chl *a* concentrations and was determined according to Eq. (1) by

$$S_{ana}^2[r(x, t)] = \frac{1}{t^2} \left[ \left( \frac{S_{ana}[C(x, t)]}{C(x, t) \cdot n_{ana}} \right)^2 + \left( \frac{S_{ana}[C(x, 0)]}{C(x, 0) \cdot n_0} \right)^2 \right] \quad (13)$$

where  $S_{ana}[C(x, t)]$  is the standard deviation of replicated chl *a* measurements and  $n_0$  and  $n_{ana}$  are numbers of initial and final measurements. The average relative standard deviation of replicated chl *a* measurements  $\{S_{ana}[C(x, t)]/C(x, t)\}$  in the observed range of 0.08 to 2.40  $\mu g$  chl *a*  $dm^{-3}$  was 2.8% of the mean sample concentration. The expected analytical variance of the apparent growth rate was  $0.00028 d^{-1}$ , equivalent to a standard deviation of  $S_{ana}[r(x)] = 0.017 d^{-1}$ .

The experimental variance of  $r(x)$  in replicated incubations was not directly observable but was inferred from the observed variance of replicates ( $S_{obs}^2$ ) by subtraction of the expected analytical component:

$$S_{exp}^2[r(x)] = S_{obs}^2[r(x)] - S_{ana}^2[r(x)] \quad (14)$$

The observed standard deviation of  $r(x)$  was  $0.026 d^{-1}$  in Series I and  $0.038 d^{-1}$  in Series II experiments; the resultant experimental standard deviations were  $0.020$  and  $0.033 d^{-1}$ , respectively, which suggests that the full nutrient amendment reduced the experimental variance.

If the model regression deviates from the true dilution response, the regression variance should be higher than the observed variance of the growth rate estimate. The magnitude of the deviation was therefore estimated from the difference between the regression variance and the observed variance of the growth rate weighted for the number of replicate experiments:

$$S_{mod}^2[\Delta r(x)] = S_{reg}^2[\Delta r(x)] - \{S_{obs}^2[r(x)]/n_{exp}\} \quad (15)$$

The estimated model deviation was equivalent to a standard deviation of  $0.008 d^{-1}$  in Series I and  $0.014 d^{-1}$

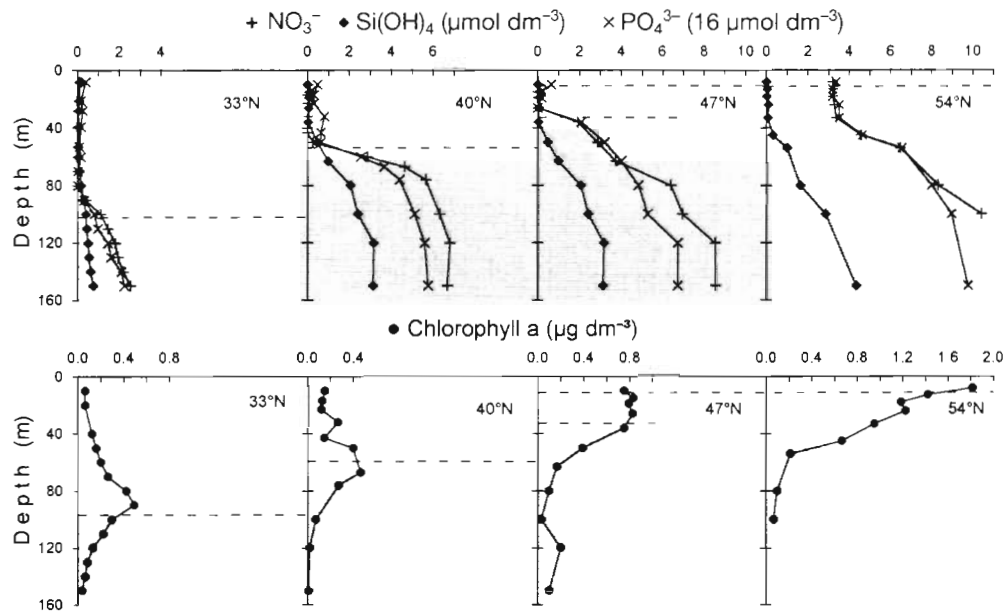


Fig. 2. Distribution of nitrate, phosphate, silicate and chlorophyll *a* at 4 sampling stations where serial dilution experiments were carried out. Dashed lines indicate the depth where seawater was sampled for incubation experiments. The upper boundary of the shaded area confines the estimated depth of the euphotic zone

in Series II experiments, indicating that this error had about the same order of magnitude as the growth rate estimates based on duplicate experiments, each 3 ini-

tial and 2 final chl *a* measurements, which accounted for an observed standard deviation in Series I and Series II experiments of  $S_{\text{obs}}[r(x)] = 0.013 \text{ d}^{-1}$  and  $S_{\text{obs}}[r(x)] = 0.019 \text{ d}^{-1}$ , respectively.

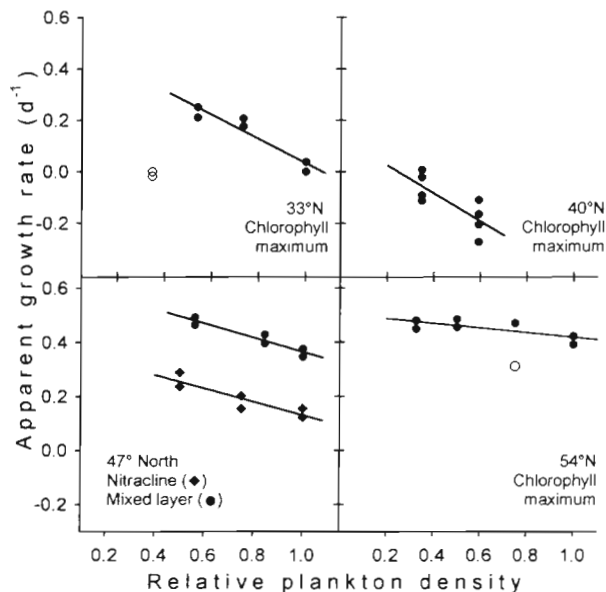


Fig. 3. Apparent growth rates as a function of relative plankton density in Series I experiments (with complete set of nutrient enrichments). The curves are fitted by least-squares linear regression of Eq. (2) according to Landry & Hassett (1982). Open symbols represent cases that were excluded from the linear regression

#### Ambient nutrient and chl *a* concentrations

As shown in Fig. 2, nitrate, phosphate and silicate were depleted in the upper mixed layer at all stations except for 54° N, where only silicate was depleted (Table 1). The depth of the chl *a* maximum shoaled along this gradient from 85 m at the southernmost station to the surface at 54° N. The chl *a* concentration at 54° N reached  $1.82 \mu\text{g dm}^{-3}$ , indicating moderate bloom conditions as compared to earlier observations in the northeast Atlantic (Lochte et al. 1993).

#### Phytoplankton growth and microzooplankton grazing

In all experiments with complete nutrient enrichment (Series I) phytoplankton growth showed a positive response to the relaxation of grazing pressure due to seawater dilution (Fig. 3). We found 1 exception to this response in the highest dilution at 33° N. This might be caused by insufficient regeneration of micro-nutrients or vitamins that are not added to the dilutions in Series I experiments.

Table 2. Grazing coefficients ( $g$ ) and turnover rates of the phytoplankton stock by microzooplankton grazing (Turnover) as well as potential growth rates ( $\mu_{\max}$ ) estimated according to Eq. (2) in Series I experiments with a complete set of nutrient enrichments. Ranges of confidence are given at a 5% error level.  $R^2$ : coefficient of determination and number of observations. nd: not determined

Latitude	Depth (m)	$g$ ( $d^{-1}$ )	Turnover (% $d^{-1}$ )	$\mu_{\max}$ ( $d^{-1}$ )	$R^2$ (n)
33° N	110	$0.47 \pm 0.06$	38	$0.50 \pm 0.06$	0.91 (6)
40° N	60	$0.53 \pm 0.14$	41	nd	0.56 (8)
47° N	30	$0.25 \pm 0.05$	22	$0.38 \pm 0.05$	0.81 (6)
47° N	8	$0.26 \pm 0.03$	23	$0.63 \pm 0.03$	0.99 (6)
54° N	8	$0.08 \pm 0.06$	8	$0.50 \pm 0.05$	0.62 (7)

The potential phytoplankton growth rate ( $\mu_{\max}$ ) from Series I experiments with full nutrient enrichments ranged from 0.38 to 0.62  $d^{-1}$  showing no latitudinal trend (Table 2). The mean phytoplankton growth rates [ $\bar{\mu}_{-N}(1)$ ] from Series II experiments without nitrogen enrichment ranged from 0.19  $d^{-1}$  at 54° N to 0.75  $d^{-1}$  at 40° N (Table 3). At the deep chlorophyll maxima of 33° N and 40° N intense microzooplankton grazing (Table 2) and high mean growth rates (Table 3) caused a high turnover of the phytoplankton stock. At 33° N the low apparent growth rate (Table 3) indicated that phytoplankton growth and microzooplankton grazing were close to a steady-state equilibrium. At 40° N we

found the highest apparent growth rate of phytoplankton of 0.23  $d^{-1}$  and the highest turnover of the phytoplankton stock by microzooplankton grazing. However, in terms of the apparent growth yield of phytoplankton we found the maximum of 0.19  $\mu g$  chl  $a$   $dm^{-3} d^{-1}$  at the bloom situation of 54° N, where it coincided with the lowest turnover of the phytoplankton stock by microzooplankton grazing (Tables 2 & 3). Estimates of the microzooplankton grazing coefficient ranged from  $g = 0.08 d^{-1}$  (equivalent to a turnover of 7.6% standing stock  $d^{-1}$ ) at 54° N, to  $g = 0.53 d^{-1}$  (equivalent to a turnover of 41% standing stock  $d^{-1}$ ) at 40° N (Table 2). In cases where regeneration did not significantly contribute to the growth yield of phytoplankton the biomass loss due to microzooplankton grazing ( $B_G$ ) did not exceed the growth yield from external and cellular nitrogen ( $B_{Di} + B_{Ed}$ ), whereas in cases where regeneration significantly contributed to nitrogen supply of phytoplankton growth  $B_G$  accounted for about 270, 670 and 1590% of the growth yield from external and cellular nitrogen (Tables 4 & 5).

#### Nitrogen supply of phytoplankton growth

In 3 of 5 experiments the regeneration by microzooplankton grazing was an important source of nitrogen supply for phytoplankton growth (Table 4). At 33° N

Table 3. *In situ* temperature ( $T_{is}$ ), *in vitro* temperature ( $T_{iv}$ ) and average *in vitro* irradiance in the photosynthetically active range ( $I_{iv}$ ) during incubation; estimates of apparent growth rates ( $r_{-N}$ ), apparent growth yields ( $r'_{-N}$ ), mean growth rates ( $\bar{\mu}_{-N}$ ) and nitrogen saturation of phytoplankton growth ( $Q_N$ ) at ambient nitrogen concentration. Ranges of confidence for  $\bar{\mu}_{-N}$  are given at a 5% error level. \* $Q_N$  values significantly below 1.  $R^2$  (n): coefficient of determination and number of observations for growth rate estimates. nd: not determined

Latitude	Depth (m)	$T_{is}$ (°C)	$T_{iv}$ (°C)	$I_{iv}$ ( $\mu E m^{-2} s^{-1}$ )	$r_{-N}$ ( $d^{-1}$ )	$r'_{-N}$ ( $\mu g$ chl $a$ $dm^{-3} d^{-1}$ )	$\bar{\mu}_{-N}$ ( $d^{-1}$ )	$Q_N$	$R^2$ (n)
33° N	110	18.2	21	5.8	0.03	0.01	$0.50 \pm 0.08$	1.00	0.97 (8)
40° N	60	14.7	19	14.1	0.23	0.10	$0.75 \pm 0.11$	nd	0.65 (8)
47° N	30	14.2	16	16.7	0.11	0.10	$0.35 \pm 0.03$	0.93	0.78 (6)
47° N	8	16.5	15	128	0.13	0.14	$0.40 \pm 0.04$	0.63*	0.97 (8)
54° N	8	12.5	13	107	0.12	0.19	$0.19 \pm 0.03$	0.39*	0.65 (8)

Table 4. Specific growth yields from regenerated ( $K_R$ ), density independent ( $K_{Di}$ ) and deficient external ( $K_{Ed}$ ) nitrogen sources in Series II experiments without nitrogen supplements, also expressed as the fraction of the total specific growth yield,  $\Sigma K = K_R + K_{Di} + K_{Ed}$ . Ranges of confidence are given at a 5% error level.  $R^2$  (n): coefficient of determination and number of observations. ns: not significant

Latitude	Depth (m)	$K_{Di}$ ( $d^{-1}$ )	$K_{Ed}$ ( $d^{-1}$ )	$K_R$ ( $d^{-1}$ )	$K_{Di}:\Sigma K$ (%)	$K_{Ed}:\Sigma K$ (%)	$K_R:\Sigma K$ (%)	$R^2$ (n)
33° N	110	$0.04 \pm 0.16$	ns	$0.61 \pm 0.18$	6.1	ns	93.9	0.97 (8)
40° N	60	$0.13 \pm 0.07$	ns	$0.99 \pm 0.22$	11.6	ns	88.4	0.65 (8)
47° N	30	$0.37 \pm 0.07$	$0.06 \pm 0.07$	ns	86.2	13.8	ns	0.78 (6)
47° N	8	ns	$0.12 \pm 0.13$	$0.36 \pm 0.09$	ns	25.6	74.4	0.97 (8)
54° N	8	$0.13 \pm 0.07$	$0.09 \pm 0.05$	ns	60.4	39.6	ns	0.65 (8)

Table 5. Total biomass losses of phytoplankton due to microzooplankton grazing ( $B_G$ ), growth yields from regenerated nitrogen ( $B_R$ ) and from cellular and external nitrogen sources ( $B_{Di} + B_{Ed}$ ). Recycling efficiency of the microbial community ( $B_R:B_G$ ) and the ratio of biomass lost due to microzooplankton grazing and biomass yielded from external and cellular nitrogen sources [ $B_G:(B_{Di} + B_{Ed})$ ]. Ranges of confidence are given at a 5% error level. \*Significantly above or below 100%. ns: not significant

Latitude	Depth (m)	$B_G$ ( $\mu\text{g chl } a \text{ dm}^{-3} \text{ d}^{-1}$ )	$B_R$ ( $\mu\text{g chl } a \text{ dm}^{-3} \text{ d}^{-1}$ )	$B_{Di} + B_{Ed}$ ( $\mu\text{g chl } a \text{ dm}^{-3} \text{ d}^{-1}$ )	$B_R:B_G$ (%)	$B_G:(B_{Di} + B_{Ed})$ (%)
33° N	110	$0.13 \pm 0.02$	$0.13 \pm 0.04$	$0.01 \pm 0.00$	99	1590*
40° N	60	$0.34 \pm 0.11$	$0.38 \pm 0.09$	$0.05 \pm 0.03$	115	670*
47° N	30	$0.30 \pm 0.06$	ns	$0.40 \pm 0.13$	ns	74
47° N	8	$0.33 \pm 0.05$	$0.36 \pm 0.09$	$0.12 \pm 0.13$	107	271*
54° N	8	$0.15 \pm 0.11$	ns	$0.34 \pm 0.19$	ns	43*

we estimated that nitrogen regeneration by microzooplankton grazing contributed about 94% of the nitrogen supply of phytoplankton growth; another 6% was supplied by external and cellular nitrogen sources. The dilution response of the mean growth rate in our experiments at 40° N (Fig. 4) indicated a threshold for nutrient regeneration (Case C\*, Fig. 1). Physiologically sensible estimates of the growth coefficients could be made by applying the model by Andersen et al. (1991) with the refinements described in Eq. (9). We estimated that regeneration contributed about 88% of the nitrogen demand of phytoplankton growth; a further 12% was supplied by external and cellular nitrogen sources. The threshold (s) was determined at a relative plankton density of about 0.69. At 47° N we incubated

water from the nitrate depleted upper mixed layer and from the nitracline with a nitrate concentration of  $1.3 \mu\text{mol dm}^{-3}$ . In the upper mixed layer nitrogen regeneration by microzooplankton grazing contributed about 74% to the nitrogen supply of phytoplankton growth, whereas at the nitracline nitrogen regeneration was not detectable, but about 86% of the phytoplankton growth yield was supplied by external or cellular nitrogen sources. From our experiments at 54° N we estimated that external and cellular nitrogen sources supplied about 60% of the nitrogen for phytoplankton growth, the remainder was contributed by a deficient external nitrogen pool. Nitrogen regeneration at this station was not detectable. In cases where nitrogen regeneration significantly contributed to nitrogen supply of phytoplankton growth, the recycling efficiency ( $B_R:B_G$ ) was about 99, 115 and 107% (Table 5).

Low values of  $Q_N$  (Table 3) indicated that the nitrogen supply of phytoplankton growth was subsaturated and that nutrient supply controlled growth at the upper mixed layer of 47° N ( $Q_N = 0.63$ ) where all macro-nutrients were depleted, and at 54° N ( $Q_N = 0.39$ ) where only silicate was depleted. Nitrogen enrichments could not significantly stimulate growth of phytoplankton from the nitracline of 47° N ( $Q_N = 0.93$ ) and the deep chlorophyll maximum of 33° N ( $Q_N = 1.00$ ), indicating that nitrogen supply was saturated and did not control phytoplankton growth.

## DISCUSSION

We used the relative plankton density ( $x$ ) as a proxy of the relative grazing activity *sensu* Landry et al. (1995). Landry (1993) first substituted this proxy by an average of initial and final grazer abundance at each dilution level. Later Landry et al. (1995) estimated the relative grazing intensity from the disappearance of fluorescent labelled cells. However, the relative plankton density ( $x$ ) is directly proportional to the relative grazing activity even if the grazer abundance or graz-

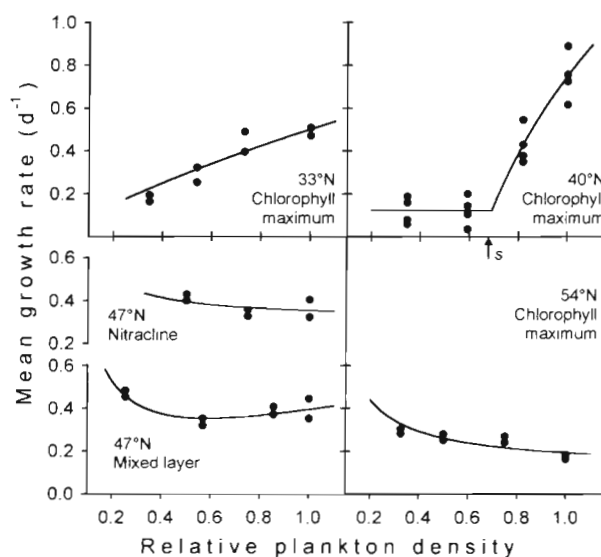


Fig. 4. Mean growth rates as a function of the relative plankton density in Series II experiments (without nitrogen enrichments). The curves are fitted by regressions according to Eq. (9), which derived from a modification of the non-linear model of Andersen et al. (1991). Arrow indicates a regeneration threshold (s)



ing activity changes during the incubation; it is therefore a suitable proxy of the relative grazing activity, provided the magnitude of changes is equal at all chosen dilution levels. Furthermore, the average grazer abundance and the disappearance of fluorescently labelled cells are themselves proxies of the relative grazing activity, because a necessarily sharp separation of herbi-, bacteri- or carnivorous taxa for determining the average grazer abundance is hardly practicable, also because different grazers may have different net growth rates, different food preferences and different ingestion rates. Landry et al. (1995) compared regressions of 'apparent growth rate' versus 'relative grazing' with regressions of 'apparent growth rate' versus 'relative plankton density' and found essentially identical growth and grazing rates. Considering that it is not yet possible to actually measure herbivorous grazing *in situ*, the applied standard dilution method has presently few if any alternatives to estimate herbivorous grazing of a whole microbial community.

Although the results of our experiments only caught a glimpse of a system that undergoes strong seasonal and cyclical variations (Lochte et al. 1993) and consists of communities that virtually never reach a stable equilibrium (Scheffer 1991), it is possible to characterise some regional differences.

### Microzooplankton grazing

A prominent trend in our experiments was the southward increase in microzooplankton grazing turnover from about 8 and 23% d<sup>-1</sup> at 54° N and 47° N, respectively, to about 41 and 38% d<sup>-1</sup> at 40° N and 33° N, respectively.

At 47° N these are similar to grazing rates measured during the JGOFS NABE Experiment by Verity et al. (1993) and Burkill et al. (1993b). At a 20° W transect from 47° N to 60° N, Burkill et al. (1993b) found that the biomass losses due to microzooplankton herbivory were positively related to phytoplankton biomass as well as seawater temperature. This result is confirmed by our experiments (Fig. 5). However, we recognise that the temperature has not only a direct metabolic effect on the grazer activity but will also affect the grazing rates through the effects on community composition. However, in contrast to the results of Burkill et al. (1993b), the biomass of phytoplankton grazed by microzooplankton ( $B_G$ ) was not significantly correlated to seawater temperature or to initial standing stock of phytoplankton [ $C(1,0)$ ] in our experiments. Since  $B_G$  depends on the grazing rate and the initial phytoplankton biomass (Eq. 11), and since grazing is spatially and temporally variable, there is also little reason

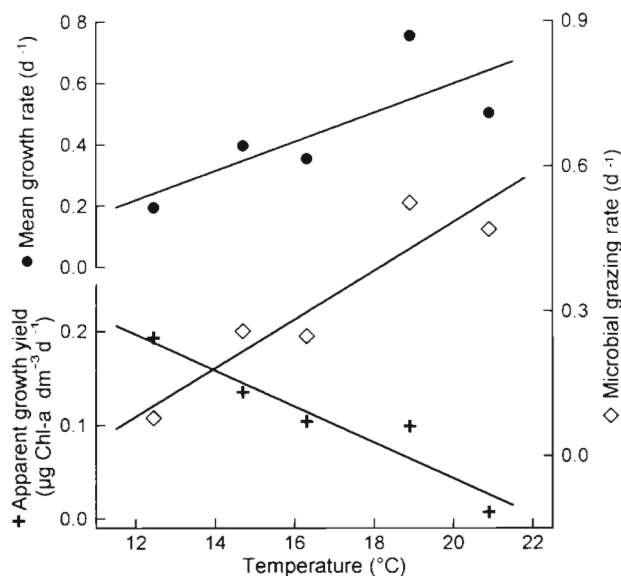


Fig. 5. Relations of mean growth rates ( $\bar{\mu}_N$ ), apparent growth yields ( $r'_N$ ) and microzooplankton grazing rates ( $g$ ) to seawater temperature ( $T_{iv}$ ) at the 20° W meridional transect from 33° N to 54° N. Regression lines are:  $\bar{\mu}_N(T_{iv}) = 0.0473[(d \cdot ^\circ C)^{-1}] \cdot T_{iv} - 0.349$ ,  $R^2 = 0.58$ ,  $n = 5$ ,  $p < 0.10$ .  $r'_N(T_{iv}) = -0.0192[\mu g \text{ chl } a (dm^3 \cdot d \cdot ^\circ C)^{-1}] \cdot T_{iv} - 0.427$ ,  $R^2 = 0.87$ ,  $n = 5$ ,  $p < 0.05$ .  $g(T_{iv}) = 0.0505[(d \cdot ^\circ C)^{-1}] \cdot T_{iv} - 0.523$ ,  $R^2 = 0.90$ ,  $n = 5$ ,  $p < 0.05$ .

to expect a relation between  $B_G$  and initial phytoplankton biomass. However, phytoplankton biomass was inversely related to the intensity of microzooplankton grazing in our study (Fig. 6), which supports the idea that microzooplankton grazing may limit the accumulation of phytoplankton biomass.

**Mean growth rates** in our experiments were not related to the amount of light received during incubation (Table 3) or to ambient nitrate concentrations (Table 1), but they significantly increased with increase in seawater temperature and intensity of microzooplankton grazing (Figs. 5 & 6). The temperature dependency may directly result from the effect on the growth metabolism whereas the relation to microzooplankton grazing is probably a coincidental effect of the temperature increase of grazing.

**Nitrogen supply** from external plus cellular nitrogen sources was also not related to the ambient nitrate concentration in our experiments, as seen by the predominant utilisation of regenerated nitrogen in the presence of medium and high nitrate concentration at the deep chlorophyll maxima of 40° N and 33° N. We suggest that this is due to preferential uptake of ammonium over nitrate, which is generally attributed to additional energy needed for nitrate reduction (Syrett 1981) and to higher metabolic costs for active nitrate transport (Turpin 1991). The predominant utilisation of

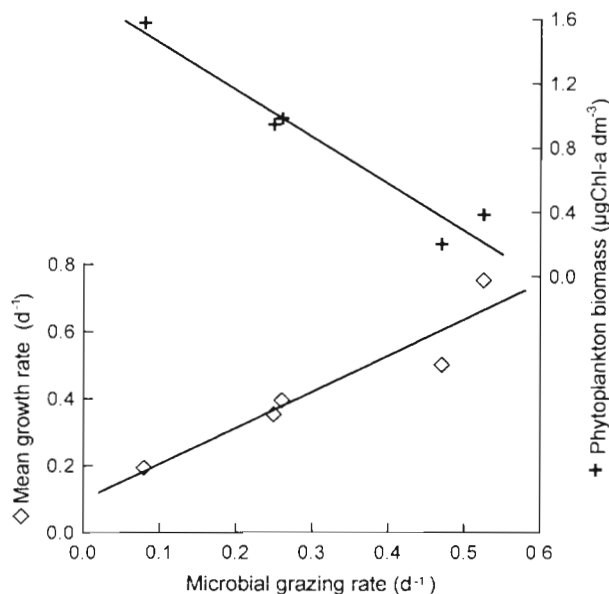


Fig. 6. Relations of mean growth rate ( $\mu_N$ ) and phytoplankton biomass ( $C$ ) to microzooplankton grazing rates ( $g$ ) on the 20° W meridional transect from 33° N to 54° N. Regression lines are:  $\hat{\mu}_N(g) = 1.08 \cdot g + 0.0978$ ,  $R^2 = 0.89$ ,  $n = 5$ ,  $p < 0.05$ .  $C(g) = 2.92 \cdot g + 1.75$ ,  $R^2 = 0.94$ ,  $n = 5$ ,  $p < 0.01$

regenerated nitrogen at low light conditions in our experiments with phytoplankton from the deep chlorophyll maxima of 40° N and 33° N is in accordance with the review by Dortch (1990), who concluded that preference for ammonium is enhanced at low light conditions.

#### Factors controlling phytoplankton growth

Light limitation at the deep chlorophyll maximum at 33° N was indicated by, (1) complete nitrogen saturation ( $Q_N = 1.00$ ), (2) high nutrient concentration and (3) the composition of the coccolithophore community (Gaul unpubl.) which consisted of a characteristic 'floriform' deep-water assemblage (*Florisphaera profunda*, *Algirospira oryza* and *Thorosphaera flabelata*) that is well adapted to extreme low light conditions (Young 1994). The subsaturated nitrogen supply of phytoplankton growth ( $Q_N = 0.63$ ) at ~50% surface irradiance and virtually depleted nutrient stocks indicated that nutrient supply rather than light controlled phytoplankton growth in the upper mixed layer at 47° N. The system at 40° N ranged between the nutrient-controlled system of the mixed layer at 47° N and the light-limited system at 33° N, according to nitrate concentration, apparent phytoplankton growth yield and depth of the chlorophyll maximum and the nitracline. The chlorophyll maximum at 40° N deepens in

the course of the season due to nutrient sequestration and may approach a state similar to that observed at 33° N later in the season (Strass & Woods 1991).

At the nitracline of 47° N phytoplankton growth at ~6.8% surface irradiance was nitrogen saturated. However as silicate was just above the detection level, light was probably co-limiting with silicate. Silicate was below the detection within the upper mixed layer of 54° N, whereas the ambient nitrate concentration was high as compared to half saturation constants of phytoplankton growth (Epplly et al. 1969). However the nitrogen supply was seriously subsaturated ( $Q_N = 0.39$ ), indicating that phytoplankton growth was nutrient limited. In spite of nutrient deficiency, we found the highest apparent growth yield of phytoplankton at the upper mixed layer of 47° N and 54° N (Table 3).

#### Recycling efficiency

In cases where the supply of regenerated nitrogen was significant, the growth yields of phytoplankton from regenerated nitrogen ( $B_R$ ) accounted for about 99, 115 and 107% of the total biomass loss from microzooplankton grazing ( $B_G$ ), indicating that microheterotrophs provided as much regenerated nitrogen for phytoplankton growth as they removed by grazing. This is in conflict with the low regeneration efficiency of protozoa and other microheterotrophs, which rarely exceeds 50% (Harrison 1992) and decreases significantly at higher growth rates and by nitrogen-deficient prey (Caron & Goldman 1990). Clearly an additional internally regenerated nitrogen source must be evoked to explain the high recycling efficiencies in our experiments.

First, the efficiency of nutrient regeneration significantly increases with the number of successive grazing and nutrient regeneration steps (Goldman et al. 1985, Suzuki et al. 1996); however at individual regeneration efficiencies of 30%, more than 7 trophic levels are required to achieve a recycling efficiency of 75% (King 1987). Thus even an extended herbivorous food chain with multiple grazing steps is probably not sufficient to explain recycling efficiencies of about 100%, also because a part of the nitrogen which is released by grazers may consist of particulate or highmolecular organic compounds which cannot be assimilated by phytoplankton (Antia et al. 1991).

However, pelagic marine bacteria principally degrade all autochthonous nitrogen compounds (Schut et al. 1997), and once nitrogen is bound in bacterial biomass it is rapidly regenerated by bacterivorous flagellates (Goldman & Dennett 1991, Miller et al. 1995). The bacterivorous grazers also effectively control the abundance of bacteria in oligotrophic environments (Ander-

sen & Fenchel 1985, Berninger et al. 1991); the bacterivorous nitrogen regeneration may therefore substantially increase the recycling efficiency through mineralisation of organic nitrogen that is lost from the herbivorous regeneration cycle. Finally mixotrophic nutrition, which is widespread among marine protists (Borass et al. 1988, Sanders 1991), may also increase the recycling efficiency since this is a highly efficient strategy to acquire nutrients bound in microbial biomass and is primarily independent of a herbivorous grazing loss.

The principal sources which supply regenerated nitrogen for phytoplankton growth are: (1) regeneration due to herbivory, (2) regeneration due to bacterivory, (3) regeneration due to carnivory and cannibalism among heterotrophic protista, (4) bacterivorous mixotrophy, (5) carnivorous mixotrophy, (6) herbivorous mixotrophy of phytoplankton, (7) viral lysis of bacteria or phytoplankton, and (8) proteolytic decay of particulate organic nitrogen. Since nitrogen regeneration is dominated by phagotrophic processes (sources 1 to 6), it depends on the density of the grazers as well as their food sources and will principally respond to dilution like  $\Delta C_R$  in Eq. (6). Therefore the dilution approach of Andersen et al. (1991) provides a method for estimating the total growth yield of phagotrophically regenerated nitrogen and assessing the regeneration efficiency of the microbial community at the basis of a full regeneration cycle, i.e. from the consumption of phytoplankton biomass ( $B_G$ ) via the release and subsequent uptake of dissolved or particulate nitrogen to the synthesis of phytoplankton biomass ( $B_R$ ).

We also calculated recycling efficiencies from data given in the original publication by Andersen et al. (1991) for oligotrophic coastal waters of the Oslofjord, southern Norway. The estimated recycling efficiencies under conditions of predominantly regenerated nitrogen supply were about 69, 65 and 59%, which are notably lower compared to our estimates of recycling efficiencies for the subtropical northeast Atlantic (Table 5); nevertheless, they also exceed average regeneration efficiencies of microheterotrophs. The apparent contradiction of low regeneration efficiencies at the species level and high recycling efficiencies at the community level can only be resolved if, apart from nutrient recycling at successive grazing steps, tight coupling of herbivorous and bacterivorous nutrient recycling is considered.

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